

Paleotemperature Estimates for the Lowland Americas Between 30°S and 30°N at the Last Glacial Maximum

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Abstract

Paleoecological data for the lowland neotropics and subtropics between 30°N and 30°S are compiled to provide an overview of climatic conditions at the time of the last glacial maximum. A clear consensus emerges from both fossil pollen and noble gas proxies that low-

Resumen

Los datos paleoclimáticos de las zonas bajas neotropicales entre los 30°N y 30°S han sido recogidos para proporcionar una sinopsis de las condiciones climáticas en tiempos del último máximo glacial. Un evidente consenso aparece con datos de polen fósil y de gases

17.1. INTRODUCTION

An accurate representation of the temperature gradients from the poles to the equator is fundamental to deriving reliable climate models. A persistent problem for modelers is to establish appropriate temperature gradients for the past. It is probably fair to say that both research effort and confidence in paleotemperature reconstructions are positively correlated with increasing latitude. Robust temperature reconstructions for the last 18,000 years at high latitudes are based on core records from deep ocean sediment, ice caps, and lake sediments. In the midlatitudes of the Americas (30°–70°N), an abundance of marine oxygen isotope and foraminiferal records provide data on past sea surface temperature (SST) (e.g., Broecker, 1986; CLIMAP Project Members, 1976, 1981). Terrestrial and nearshore sedimentary records have drawn on a wide array of proxy indicators that provide paleotemperature records for the land (e.g., Davis, 1981; Webb, 1987; Heusser, 1995; Haberle, 1998; Smith and Betancourt, 1998). On the whole, the temperature reconstructions of midlatitude terrestrial and oceanic systems are in close agreement (e.g., CLIMAP Project Members, 1981; Kutzbach and Guetter, 1986). In South America, at equivalent latitudes, a growing body of palynological, glaciological, and entomological data provide convincing paleotemperature reconstructions from the present to 18,000 ¹⁴C B.P. (e.g., Markgraf, 1993). However, comparatively few records from nearshore or terrestrial environments are available for the subtropics to the equator (30°–0°) in either hemisphere.

Paleoclimate data for tropical regions began to appear in the 1960s with fossil pollen records from montane Colombia (van der Hammen and Gonzalez, 1960) and Costa Rica (Martin, 1964). Mercer began investigations of relict moraines in Peru (e.g., Mercer and Palacios, 1977) and spawned an active field of Andean moraine-based reconstructions of high-elevation cooling (e.g., Clapperton, 1987; Seltzer, 1990). In the 1980s, further data were gathered from the Sabana de Bogotá and other sites in Andean Colombia (Hooghiemstra, 1984, 1989) and the Junín Plateau of Peru (Hansen et al., 1984). By the mid-1980s, a consensus emerged of high-elevation cooling during glacial times. Some glaciological data from Ecuador suggested that mid-Pleistocene (ca. 40,000–30,000 ¹⁴C B.P.) ice advances had pushed further downslope than those of 18,000 ¹⁴C B.P. (Clapperton, 1987). However, it was not clear whether these lowermost moraines were the product of lower temperatures or greater moisture availability. Van der Hammen and Hooghiemstra (2000) suggest a cooling of ca. 8°C in the Andes at 18,000 ¹⁴C B.P. and suggest that this was the coolest period documented in the late Pleistocene at the Sabana de Bogotá.

The CLIMAP (1976) SST estimates coincided with conventional biogeographic wisdom (e.g., Haffer, 1969; Vanzolini, 1970), which demanded that lowland tropical temperatures remained constant, or nearly so, during glacial cycles. However, this hypothesis remained untested because of logistic difficulties and technical doubts about the feasibility of lowland tropical palynology (Faegri, 1966). The first data that provided a glimpse of glacial conditions from the lowland neotropics were equivocal.

Van der Hammen and his team pioneered lowland palynology in South America with core sections from Ogle Bridge, Guyana, and the Alliance Borehole, Surinam (van der Hammen, 1963, 1974; Wijmstra, 1969). In both sequences the records show Poaceae-rich pollen spectra replacing mangrove and mesic forest pollen. A reasonable interpretation is that closed forest was replaced by more xeric communities. However, as neither sequence is dated (apart from one date of >45,000 ¹⁴C B.P.), it is impossible to assign these spectra to any particular pre-Holocene interval. Similarly, two undated diagrams from Rondônia on the southern fringe of forested Amazonia apparently depict a northward range expansion of savanna elements. Absy and van der Hammen (1976) attributed the savanna expansion to glacial age aridity. Though tantalizing, these data sets did not provide reliable climatic data for the last glacial period. Better evidence for Pleistocene drying came from the Lake Valencia record, Venezuela, which suggests climates were cooler and drier during glacial times than now (Bradbury et al., 1981).

In this chapter, we provide an overview of a growing body of well-dated paleoecological data for the lowland (<1200 m elevation) neotropics and provide a consensus estimate of lowland neotropical paleotemperature at 18,000 ¹⁴C B.P.

17.2 METHODS

The principal techniques used to date in reconstructions of terrestrial paleotemperatures for the lowland neotropics have been pollen in lake sediments and noble gases dissolved in groundwater. The collection and processing of pollen samples are broadly standardized around the techniques outlined by Faegri and Iversen (1989). The area of methodology that is worthy of review is in the quantification of paleotemperature.

Lowland palynological temperature reconstructions are generally based on the movement of indicator taxa. Apparently, stenothermic pollen taxa, or ones that at least occupy identifiable habitat ranges, are selected as

indicator species. The modern range of these taxa is then compared with past ranges, and from this an inference is made about past climate. Van der Hammen and Gonzalez (1960) were the first researchers to correlate the downslope movement of pollen taxa to changes in temperature. They achieved this translation through the application of moist air adiabatic lapse rates. For instance, if in the past a species was documented 1000 m downslope of its present position, and the local moist air adiabatic lapse rate was 5°C of cooling per 1000 m of ascent, the paleotemperature change was 5°C cooler than present values.

Most researchers have since adopted this method of calculating temperature change, but we should examine some of its assumptions.

The first assumption is that there has been no significant evolutionary change in the requirements of the pollen taxa. Given the short time interval (20–50 tree generations since the last glacial interval), it is unlikely that evolution is a major problem, especially when more than one pollen taxon is exhibiting the same trend.

A second assumption is that the moist air adiabatic lapse rate has not changed. Studies of moist air adiabatic lapse rates reveal that they are rigidly constrained by the physical properties of air and are unlikely to have wavered outside of a narrow range (Webster and Streten, 1978; Rind and Peteet, 1985). Moist air associated with cloud forests and the wet lowland forests has a lapse rate of ca. 5°C. At the other extreme, desert dry air can have lapse rates approaching 7°C (Webster and Streten, 1978). Thus, the greatest potential change would be 2°C/1000 m of ascent. For many years, changes in ice age lapse rates were used to explain the anomalously warm oceans compared with the cool Andes (e.g., Haffer, 1991). However, as will be demonstrated later, when there is evidence of cooling, the forests are mesic or humid, indicating the presence of moist air. In other words, the *Alnus*, *Hedyosmum*, *Weinmannia*, *Podocarpus*, and *Drimys* populations that spilled down the flank of the Andes were of species adapted to the moist conditions of the cloud forest in which they now live. With paleoecological evidence to show that elevations as low as 1000 m above sea level (asl) had saturated air, it is not possible to discount evidence of cooling on the basis of steepened lapse rates.

A further criticism of using pollen to describe annual average paleotemperature is that the range of plants (therefore the elevation at which they grow) is determined not by mean annual temperatures, but by absolute minima. The distribution of plants is determined by the coldest night they survive rather than mean temperature. One way to test whether observing minimum temperatures rather than mean temperatures would

yield more information on species ranges is to plot both mean and minima data against elevation, and fit a regression line for each set of values. If the regression lines have a similar slope, then it is legitimate to use plant ranges to derive mean temperature values. Of course, the minima are likely to be more ecologically revealing in terms of determining the cause of the distribution, but that is a separate issue.

Detailed long-term climatic data on temperature maxima and minima are scarce for the neotropics, but a data set that provides a transect of daily minimum temperatures from Manaus, across lowland Ecuador, to the crest of the Andes is shown in Fig. 1. This data set is far from perfect, and some records were kept for only a few years. A relatively short run of data will not affect the mean temperature values, but may underestimate occasional bouts of extreme cooling. However, the lowland records did include an episode of *friagem* cooling, and it is unlikely that much lower temperatures would be experienced under modern conditions. As a first approximation, this data set clearly makes the point that tropical temperature minima are generally closely correlated to mean temperatures.

Climatic requirements of *Araucaria*—e.g., mean winter temperature, number of days of frost, and length of dry season—are used by Ledru (1991, 1992, 1993) and De Oliveira (1992) to infer paleoclimates associated with a Pleistocene range expansion of this genus. If it is assumed that *Araucaria* distributions are bound by these variables, a comparison of climatic data from the modern range with that of the Pleistocene range pro-

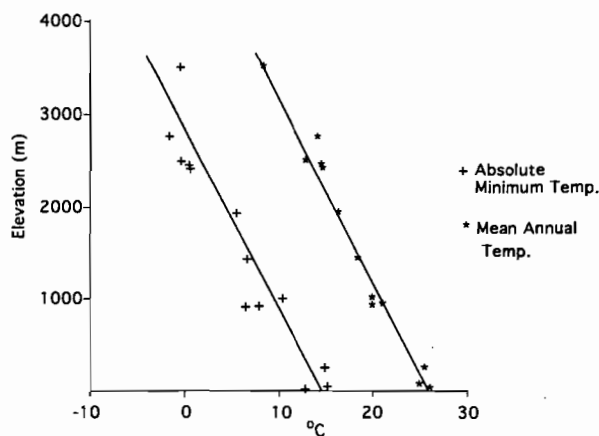


FIGURE 1 Modern mean annual and minimum temperatures for Ecuadorian weather stations (Centro Ecuatoriano de Investigación Geográfica [CEDIG] 1983) plotted against elevation. The regression line through the mean temperature data represents a 5°C/1000 m ascent, representing moist air adiabatic lapse rate. The line through the minima data represents a best-fit regression line. Note how the two lines for minimum and mean temperatures are virtually parallel.

vides estimates of changes in temperature and precipitation. This technique is freed from assumptions about lapse rates and, therefore, provides a valuable alternate means to measure paleotemperature. The above-cited authors used the movement or expansion of *Araucaria* forest from southern into southeastern Brazil (20°–25°S) to infer past-climate change. Behling and Lichte (1997) adopted a similar technique as they documented the movement, or expansion, of subtropical grassland from southern into southeastern Brazil. They found Pleistocene assemblages rich in subtropical grassland species approximately 7° of latitude farther north than their present range. Basing their climatic inference on modern weather data for the two areas, they infer an ice age cooling of between 4° and 8°C.

Another way to assess temperature using whole community values rather than indicator species has formed the basis of conventional transfer functions (e.g., Imbrie and Kipp, 1971; CLIMAP Project Members, 1976; Bonnefille et al., 1990). A number of problems are inherent in this approach, such as the lack of modern analogs for past assemblages and an inherent tendency toward underestimating any change. Many pollen taxa within an assemblage provide no detailed climatic information and can be regarded as catholic. If a full range of analog sites existed, the diluting effect of many catholic species would not matter, but without a full array of analogs, the presence of catholic species inevitably moderates the signal of climate change. The solution is to exclude the catholic species from the analysis and use a selection of stenothermic species. This compromise between using single indicator species and whole communities can be used to estimate response surfaces for precipitation or temperature. This technique could provide a paleothermometer that is independent of lapse rates.

It has been suggested that biome boundaries could be used to model past-climate change. The strength of the biome approach is that it is independent of lapse rates, it does not rely on modern communities being exactly those of the past (though intermediate vegetation types between recognizable modern biome types are a problem), and it should reduce subjectivity in interpretation. However, this technique also has problems that are particularly severe in the tropical lowlands (Marchant et al., in press).

Biome models assume that there will always be a biome to replace the existing one, but in the case of the lowland tropics there is none. Applying such models to lowland tropical paleoecology brings into focus a philosophical problem inherent in the concept of the biome—that modern conditions are normal. But, they are not. Glacial age conditions were the norm of the last 2 million years, and modern times are oppressively hot.

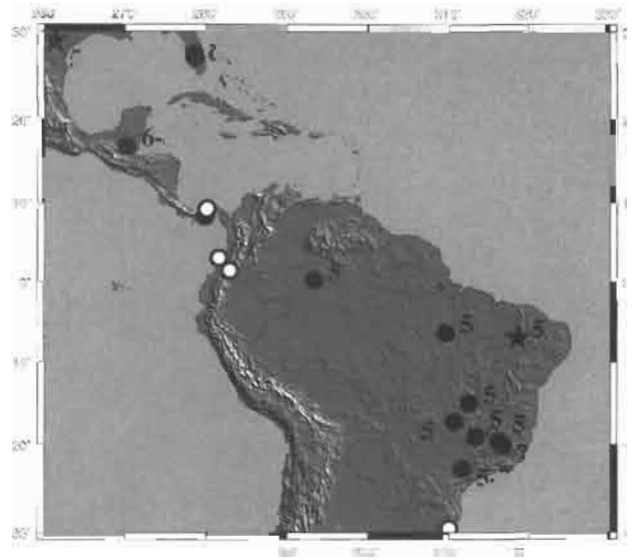
At 0° latitude and at 50 m elevation in the middle of the vast Amazonian plain, there is nowhere to retreat when it gets warmer. Some of the most stenothermic species that flanked the Andes escaped upslope to cooler climates at the beginning of the Holocene and will stay there until normal conditions return. The majority of species stay where they are because there are no *hotter adapted* species to displace them. Thus, the lowland tropics are unique—they really cannot show a warmer than usual signal (remember glacial conditions are the norm), other than an upslope migration of a few species. Biome models may be more appropriate in other settings, but they will fail in the lowland tropics because the lowland tropic biome is an endpoint in the biome continuum.

A second problem with taking the results of biome models at face value is more mechanical. Because the models treat a biome as a uniform climatic mass, the only changes indicated are when one biome replaces another. In other words, two regions that occur within the same biome—say, Atlanta and New York, which both occur in a temperate forest biome—would be accorded the same climate. It is clear that there could be substantial climatic change and yet no change in biome. Where biomes do change, relatively massive changes in climate are inferred. Neighboring areas that experience similar climatic change, but are judged to be biome constant, are suggested to have had a constant climate. Not all climate effects are geographically gradual, but we suggest the biome is too coarse a descriptive unit to elucidate paleoclimatic change in the tropics.

The only possible biome change that could be registered in Amazonia would be a transition from forest to savanna. Clearly, it is unsatisfactory to reduce all possible climatic variants to a simple "either savanna or forest." Under this kind of biome construction, vast areas will show no climatic change, and within the constructs of their model they are precisely correct. During the last glacial period, savanna did not replace large areas of forest, nor did lowland forests give way to Paramo grasslands or even to montane forest. Given the observed vegetation changes documented in the Amazon basin, over the greatest portion of the area there were no changes in biome; but this does not mean that there was not a significant change in temperature or precipitation.

17.3. NOBLE GASES DISSOLVED IN GROUNDWATER

In recent years, a new approach that provides an independent paleotemperature proxy has evolved, i.e., the measurement of atmospheric noble gases dissolved



evidence of drying during the glacial maximum at this site, it is possible that there would have been some steepening of the lapse rate. For this reason, Leyden considers the lower of these estimates to be more realistic.

The first compelling evidence that glacial cooling affected the Amazon basin came with the discovery of *Podocarpus* timber at 1100 m elevation at Mera, Ecuador (Liu and Colinvaux, 1985). Equatorial *Podocarpus* species are almost exclusively montane, seldom living at elevations lower than 1800 m. Liu and Colinvaux (1985) inferred a temperature depression of ca. 4°C for the period between 33,000 and 30,000 ¹⁴C B.P. on the basis of this evidence. A more detailed analysis of the sediments and the discovery of a second site at San Juan Bosco (970 m elevation) in Ecuador widened the list of cool indicator taxa to include *Magnolia*, *Drimys*, *Alnus*, *Hedyosmum*, *Weinmannia*, and grasses of the three-carbon (C3) photosynthetic pathway. With further dating, a cooling of 7.5°C was suggested for the period from 33,000–30,000 ¹⁴C B.P. and 4°C for the period from 30,000–26,000 ¹⁴C B.P. (Bush et al., 1990).

Since 1990, new data sets for different lowland ecosystems have produced further evidence of a substantial temperature depression during the glacial period. Lagoa Crominia in the Cerrado of central Brazil suggested a cooling of 5°C at 18,000 ¹⁴C B.P. (Ferraz-Vicentini and Salgado-Labouriau, 1996). Lagoas dos Olhos and Serra Negra (De Oliveira, 1992) and the swamp of Salitre (Ledru, 1993) all document the Pleistocene expansion of *Araucaria* forests. Records for southern Brazil indicate the expansion of subtropical grasslands (Behling and Lichte, 1997; Behling et al., 1998). In each case, a 5°C lowering of temperature during glacial times is inferred. In the lowland Amazon, lakes perched atop massifs, such as the Serra dos Carajas (Absy et al., 1991) and the Hill of Six Lakes (Colinvaux et al., 1996), have provided long records of the lowland forest environment. The Carajas record is interpreted by Absy et al. (1991) primarily in terms of wet and dry events, but the pollen record is consistent with a glacial cooling (Absy, personal communication). Two records from the Hill of Six Lakes contain significant amounts of *Podocarpus*, *Hedyosmum*, and *Weinmannia* pollen, leading to the suggestion of a 5°C glacial cooling (Colinvaux et al. 1996).

17.5. THE DATA SET TO DATE: 30°N TO 30°S

Table 1 presents a summary of available data documenting paleotemperature at 18,000 ¹⁴C B.P. for the tropical and extratropical regions of the New World.

17.6. DISCUSSION

It is evident from this data set that few records have sediments explicitly dated to 18,000 ¹⁴C B.P. Ledru (1992) and Ledru et al. (1998) have suggested that the period from ca. 25,000–16,000 ¹⁴C B.P. was a time of regionwide aridity in which most lake basins dried out. A priori arguments, such as a cooler ocean and land surface would have reduced evaporation, and hence cloud formation, and weakened circulations would have brought less moisture onshore, are powerful. Some reduction in precipitation and lake levels during the last glacial is very likely. There is no question that depositional rates slowed at a number of sites from Panama to Brazil during this period. However, more sites and better dating are needed before it can be resolved whether this period was a single phase of major widespread aridity or local asynchronous drying events.

With our paucity of sites, the vastness of the area considered, and current inability to assess paleoprecipitation from pollen records (see Colinvaux et al., 2000, for a review, and a contrasting review by Hooghiemstra and van der Hammen, 1998), it is to be expected that there will be considerable debate within our community over the extent and duration of possible dry events. Divergent views are held within this group of authors; however, none espouse such serious drying as to elevate lapse rates sufficiently to explain away the signature of cooling.

17.6.1. The Potential Influence of CO₂ and UV Radiation on Past Vegetation Assemblages

Street-Perrott et al. (1997) suggested that past concentrations of CO₂ may have been at least as important as cooling in determining the elevation at which species grew during glacial times. They suggest that under glacial conditions, with atmospheric concentrations of CO₂ close to 180 ppm, plants using the four-carbon photosynthetic pathway (C4) or crassulacean acid metabolism (CAM) would be expected to outcompete those using the C3 pathway. It has been argued that, in Africa, the lowering of tree lines apparent in some pollen records was, in part, an artifact of palynologists' inability to resolve the difference between C3 (montane) and C4 (lowland) grasses (Street-Perrott et al., 1997). Street-Perrott et al. suggest that instead of an invasion of midelevations by C3 grasses, high Poaceae pollen percentages reflect C4 grasses outcompeting seedlings of C3 trees during the glacial maximum.

The principal problem encountered by a C3 plant faced with low CO₂ concentrations is drought stress (Woodward 1993). In western Amazonia and on the

TABLE 1 Locations, Ages, and Paleotemperature Data for Lowland Neotropical Sites Used in Reconstructions of Paleotemperature at 18,000 ¹⁴C B.P.^a

Site	Latitude, longitude	Elevation (m)	Dates	Lab no.	Calibrated years B.P. min. cal. age (cal. age) max. cal. age	Delta T°C at 18,000 (21,500)	Max. cooling	Date of max. cooling	Ref.
Carrizo Aquifer (U.S.A.)	29°N, 98°40'W	-98.75	10,600 ± 3,000		19,560 (12,530) 5,300	-5	-5	Uniform throughout period considered	Stute et al., 1992 Stute and Clark, unpublished ¹⁴ C data Watts, 1975
			11,700 ± 3,000		17,600 (13,640) 9,650				
			20,800 ± 3,000		[24,400]				
			27,200 ± 3,000		[30,500]				
Lake Annie (U.S.A.)	27°12'N, 81°25'W	40	4,715 ± 95	I-6889	5,580 (5,350) 5,310	Cooler, unquantified			
			13,010 ± 165	I-6888	15,730 (15,450) 15,150				
			37,000 ± 3,200	I-6025	[38,900]				
Lake Tulane (U.S.A.)	27°35'N, 81°30'W	34	9,810 ± 90	WIS-1753	11,000 (10,990) 10,950	Cooler, unquantified			Grimm et al., 1993
			10,940 ± 120	WIS-1648	12,980 (12,860) 12,740				
			13,730 ± 130	WIS-1649	16,650 (16,460) 16,270				
			17,170 ± 210	WIS-1754	20,720 (10,350) 20,000				
			20,380 ± 239	WIS-1650	[24,000]				
			24,240 ± 400	WIS-1755	[27,700]				
			26,120 ± 440	WIS-1651	[29,500]				
			32,300 ± 450	QL-4630	[34,900]				
			35,700 ± 650	QL-4631	[37,800]				
			>33,000	WIS-1652	>[35,500]				
			35,600 ± 400	QL-4057	[37,700]				
			39,600 ± 500	QL-4058	[41,100]				
>46,000	QL-4632	>[46,600]							
Quexil (Guatemala)	16°55'N, 89°49'W	110	10,750 ± 460	SI-5257	13,120 (12,680) 12,130	-6 to -8	-6.5 to -8	24,000 (27,500) to 14,000 (16,800)	Leyden et al., (1993)
			10,300 ± 110	AA-3062	12,330 (12,150) 11,900				
			10,630 ± 110	AA-3063	12,680 (12,560) 12,420				
			12,790 ± 60	b-92902	15,270 (15,100) 14,910				
			27,450 ± 500	AA-3064	[30,800]				
Lake Gatún (Panama)	9°16'N, 79°52'W	-30	9,600 ± 300	UCLA-185	11,000 (10,750) 10,220	N/A	-2.5 reinterpreted as -5	11,000 (12,900) to 10,000 (11,200)	Bartlett and Barghoorn, 1973
			11,300 ± 200	UCLA-186	13,430 (13,210) 13,010				
	35,500 ± 2,500	UCLA-1025	[37,600]						
La Yeguada (Panama)	8°27'N, 80°51'W	650	8,840 ± 130	b-26102	9,970 (9,880) 9,650	N/A	-6	14,000 (16,800) to 12,000 (14,000)	Bush et al., 1992
			10,210 ± 130	b-25923	12,240 (11,980) 11,340				
			10,530 ± 100	b-24739	12,580 (12,450) 12,310				
			11,250 ± 140	b-24738	13,310 (13,160) 13,010				
			11,610 ± 180	b-25924	13,770 (13,160) 13,330				
			14,230 ± 370	b-25925	17,490 (17,060) 16,610				
			13,670 ± 210	b-25696	16,660 (14,430) 13,830				
			12,910 ± 140	b-24241	15,340 (15,290) 15,020				

(continues)

TABLE 1 (continued)

Site	Latitude, longitude	Elevation (m)	Dates	Lab no.	Calibrated years B.P. min. cal. age (cal. age) max. cal. age	Delta T°C at 18,000 (21,500)	Max. cooling	Date of max. cooling	Ref.
El Valle (Panama)	8°20'N, 80°10'W	500	8,330 ± 150	b-27721	9,450 (9,370) 9,040	-4	-6	14,000 (16,800)	Bush and Colinvaux, 1990
			14,180 ± 250	b-29038	17,300 (17,000) 16,700				
			19,420 ± 330	b-27722	[23,100]				
			31,850 ± 1,800	b-27723	[34,500]				
San Juan Bosco (Ecuador)	3°3'N, 78°27'W	970	>35,000	b-27724	>[37,200]	N/A	-7.5	ca. 33,000 (35,500)	Bush et al., 1990
			30,720 ± 800	b-25697	[33,600]				
			26,020 ± 300	b-27144	[29,400]				
			30,990 ± 350	b-27145	[33,800]				
Mera (Ecuador)	1°29'N, 77°06'W	1100	26,530 ± 270	b-10170	[29,600]	N/A	-7.5	33,000 (35,500)	Bush et al., 1990
			31,870 ± 970	b-27143	[34,500]				
			33,520 ± 1,010	b-9618	[35,900]				
Lagoa Pata (Brazil)	0°16'N, 66°41'W	250-300	5,800 ± 70	b-63417	6,720 (6,630) 6,490	-5	-5	14,000 (16,800)	Colinvaux et al., 1996
			14,230 ± 60	b-91489	17,170 (17,060) 16,950				
			15,560 ± 60	b-90306	18,570 (18,460) 18,360				
			17,840 ± 300	b-75109	21,700 (21,280) 20,840				
			18,020 ± 70	b-90307	21,700 (21,510) 21,320				
			30,830 ± 220	b-91490	[33,600]				
			31,390 ± 540	b-75110	[34,200]				
			32,010 ± 630	b-88941	[34,700]				
			34,650 ± 420	b-89715	[36,900]				
			37,830 ± 1,300	b-88942	[39,600]				
			38,860 ± 920	b-68529	[40,500]				
			42,010 ± 1,240	b-68530	[43,200]				
			Lagoa Verde (Brazil)	0°16'N, 66°41'W	250-300				
2,790 ± 50	CAMS- 47776	2,940 (2,860) 2,790							
12,480 ± 60	b-95704	14,800 (14,620) 14,450							
17,100 ± 70	CAMS- 47777	20,480 (20,250) 20,050							
16,410 ± 70	CAMS- 47778	19,470 (19,310) 19,170							
18,430 ± 100	b-95705	[22,200]							
19,740 ± 70	b-95706	[23,400]							
19,170 ± 120	CAMS- 47779	[22,900]							
18,680 ± 130	CAMS- 47780	[22,400]							
23,600 ± 450	OS-1320	[27,100]							
>43,800	OS-1321	>[44,700]							

Carajas (Brazil)	6°20'S, 50°25'W	700	10,460 ± 150 12,520 ± 120 22,870 ± 500 23,670 ± 500 24,520 ± 820 28,660 ± 1,000 51,200 ± 2,000		12,550 (12,370) 12,150 14,920 (14,680) 14,450 [26,400] [27,200] [28,100] [31,800] [51,200]	-5	-5	9000 (10,000)	Absy et al., 1991
Serra Grande Aq (Brazil)	7°S, 41°30'W	-41.50	13,100 ± 3,000 14,800 ± 3,000 16,000 ± 3,000		18,980 (15,590) 11,680 21,240 (17,700) 13,750 22,700 (18,860) 15,300	-5	-5	Uniform throughout period considered	Stute et al., 1995
Agguas Emendadas	15°S, 47°35'W	1040	7,220 ± 50 21,450 ± 100	OBDY 1152 OBDY 1193	8,060 (7,960) 7,930 [25,100]	-5	-5	14,000 (16,800)	Barberi et al., 1995
Crominia (Brazil)	17°17'S, 49°25'W	710	6,680 ± 90 13,150 ± 50 32,060 ± 520 32,390 ± 680 32,580 ± 1,640	UtC 45715 OBDY 956 UtC 45716 UtC 64283 UtC 45717	7,560 (7,490) 7,400 15,800 (15,670) 15,530 [34,700] [35,000] [35,100]	-5	-5	14,000 (16,800)	Ferraz- Vicentini and Salgado- Labouriau, 1996
Lagoa dos Olhos (Brazil)	19°38'S, 43°54'W	730	6,710 ± 140 15,530 ± 110 19,410 ± 160	b-53327 b-53328 b-35394	7,640 (7,540) 7,400 18,570 (18,440) 18,300 [23,100]	-5			De Oliveira, 1992
Serra Negra (Brazil)	19°S, 46°45'W	1170	14,280 ± 90 39,930 ± 540 >46,180	b-53314 b-53315 b-53321	17,250 (17,120) 16,990 [41,400] >[46,800]	-5	-5		De Oliveira, 1992
Salitre (Brazil)	19°S, 46°46'W	1050	9,150 ± 80 10,440 ± 110 10,350 ± 230 12,890 ± 80 14,230 ± 150 16,800 ± 100 28,740 ± 500 32,030 ± 500 >50,000	OBDY 570 OBDY 495 OBDY 496 OBDY 550 OBDY 571 OBDY 552 OBDY 470 OBDY 471	10,280 (10,040) 10,010 12,490 (12,350) 12,170 12,520 (12,230) 11,720 15,440 (15,260) 15,060 17,250 (17,060) 16,870 20,050 (19,820) 19,610 [31,900] [34,700] >[50,000]	-5	-5	11,000 (12,900)	Ledru, 1993
Catas Altas (Brazil)	20°05'S, 43°22'W	755	8,310 ± 295 20,490 ± 165 19,960 ± 530 21,550 ± 440 22,087 ± 1,580/ -2,190 37,880 ± 930 >47,740	Hv20825 Hv20826 Hv20827 Hv20828 Hv20829 Hv20830 Hv20831	9,520 (9,300) 8,780 [24,100] [23,600] [25,200] [25,700] [39,700] >[48,100]	-7	-7	28,000 (31,300) to 18,000 (21,500)	Behling, 1998
Botucatu (Brazil)	22°48'S, 48°23'W	770	5,678 ± 37 19,180 ± 190 25,750 ± 170 22,900 ± 130 >32,360	UtC-5544 Hv-20824 UtC-5545 UtC-5546 Hv-20824	6,490 (6,450) 6,410 [22,900] [29,200] [26,400] >[34,900]	-5 to -7	-5 to -7		Behling et al., 1998

^aCalendar ages were calculated with CALIB 3.0.3c (Stuiver and Reimer, 1993) for the interval up to 18,367 ¹⁴C.B.P. In the interval from 18,367 to 27,120 ¹⁴C B.P., a linear conversion is used assuming corresponding calendar ages of 22,115 and 27,120 cal. years B.P., respectively. The calendar ages are based on Bard et al. (1990). For the interval 27,120–50,000 ¹⁴C B.P., Mommersteeg (1998) assumes a difference of 3350 cal. years at 27,120 ¹⁴C B.P., which gradually diminished to a difference of zero calendar years at an age of 50,000 ¹⁴C B.P., based on the work of Mazuad et al. (1991) and Laj et al. (1996). Calibrated ages are shown in parentheses, flanked by a 1 sigma age range.

17.6.3. Implications of Cooled Tropical Lowlands

The descent of upland vegetation elements 1000 m below their modern limits is apparent in both high- and low-elevation pollen records at 18,000 ¹⁴C B.P. As humid conditions extended from the foot of the Andes to 2500 m elevation, it is safe to assume a lapse rate that approximated to 5°C/1000 m of ascent, and thereby a 5°C cooling. Another way to view this is that frost may have occurred as low as 800 m elevation at the equator. Other critical temperature thresholds, such as permanent damage to plant lipid membranes that occurs between 8 and 13°C (Graham and Patterson, 1982), are likely to have been experienced in all but the most sheltered locations. Cold stress would have affected populations throughout the study area, causing the re-assortment of species into unique communities. Populations at the tips of peninsulas such as Florida, on islands, and close to the equator could not have migrated to escape cold episodes and may have experienced the greatest species losses. Given that this last glacial interval was not significantly colder than those that had preceded it in the Quaternary, a wave of extinctions would not be expected. Any truly cold-intolerant species would have been eliminated by earlier glacial episodes, possibly explaining the greater diversity of Miocene than Holocene palynomorphs in Amazonia (van der Hammen and Absy, 1994). However, as in the midlatitudes, from Florida to the equator and south to the Mato Grosso, the Pleistocene landscape would have been filled with assemblages of plants and animals without modern analogs.

It is apparent that a reconciliation is needed between the marine and terrestrial records. Reconstructions of SSTs suggested that the tropical oceans adjacent to South America had barely cooled at 18,000 ¹⁴C B.P. (CLIMAP Project Members, 1981). Temperature depressions of only 1°–2°C were suggested by analysis of foraminiferal communities recovered from deep ocean cores. These reconstructions were based on the comparison of modern analog and fossil communities. At high and midlatitudes, the degree of communality (overlap of modern and fossil assemblages) was strong (approaching 100%), giving confidence to the temperature reconstructions. However, seven of nine cores within 2° latitude of the equator had statistically insignificant communality during the period 20,000–14,000 ¹⁴C B.P. (sensu Mix et al., 1986). Weak communality translated to tenuous paleoclimatic reconstructions, yet the CLIMAP (1981) tropical paleotemperatures for 18,000 ¹⁴C B.P. were widely accepted. A reevaluation of the CLIMAP data is being conducted (Alan Mix, personal communication), and these results

will be eagerly awaited by the terrestrial community. In the meantime, isotopic analyses of Pleistocene Caribbean coral reefs suggest that in these nearshore environments, SSTs were 5°C cooler than present values (Guilderson et al., 1994). A similar cooling of the sea surface was documented by using the relative abundance of double bonds in alkenones from marine sediments (Bard et al., 1997). These investigators inferred a 4°C cooling for the equatorial Atlantic at the time of the last glacial maximum and a cooling of as much as 7°C in some nearshore samples from the Caribbean.

Taking a different approach, Webb et al. (1997) maintained a modern ocean heat transport in their model of glacial SST. After allowing for reduced sea levels, lowered CO₂ concentrations, enlarged ice masses, and energy being channeled through glacial North Atlantic Intermediate Water rather than via the North Atlantic Deep Water, they predicted a 5.5°C cooling of tropical SSTs.

17.7. CONCLUSIONS

Overall, the paleoecologic and isotopic data set from the lowland neotropics reveals a remarkable constancy in the estimate of temperature for the period around 18,000 ¹⁴C B.P. In almost all cases, a cooling approximating to 5°C is recorded. It is heartening to find a growing body of independent temperature estimates emerging from the marine and modeling communities that are in close accord with the terrestrial estimates of paleotemperature. The terrestrial data also strongly suggest that brief climatic oscillations lasting a few millennia centered on 30,000 and 14,000 ¹⁴C B.P. may have produced even stronger local cooling episodes with temperatures as much as 7.5°C below present levels. Although our community is generally united in its estimate of a lowland neotropical cooling of 5°C for much of the last glacial period, it must be recognized that this is a very crude estimate. We have very few records from an enormous area, and, in many cases, the sedimentary sequences apparently contain gaps or at least rapid changes in depositional rate.

Our community is divided over the important issue of the magnitude and timing of precipitation change during glacial episodes. The forthcoming debate promises to be both vigorous and rewarding, stimulating, it is hoped, the invention of a technique to provide reliable estimates of paleoprecipitation. The only certainty that we have now is that we have too few data to address the issue in any authoritative way.

Although the potential impact of lowered concentrations of CO₂ on the success of individual species is recognized, there is no evidence to suggest that C4 or

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Interhemispheric Climate Linkages

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ACADEMIC PRESS

A Harcourt Science and Technology Company

San Diego San Francisco New York Boston London Sydney Tokyo

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Academic Press

A Harcourt Science and Technology Company
525 B Street, Suite 1900, San Diego, California 92101-4495, USA
<http://www.academicpress.com>

Academic Press

Harcourt Place, 32 Jamestown Road, London NW1 7BY, UK
<http://www.academicpress.com>

Library of Congress Catalog Card Number: 00-104375

International Standard Book Number: 0-12-472670-4

PRINTED IN THE UNITED STATES OF AMERICA

00 01 02 03 04 05 MM 9 8 7 6 5 4 3 2 1